EFFECTS OF MANURES AND FERTILIZERS ON SOIL FAUNA: A REVIEW[1]

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INTRODUCTION

Two broad categories of fertilizers are generally recognized: bulky organic manures (dung, compost, sewage sludge, sea weed) and inorganic mineral fertilizers (artificial, commercial or chemical). Manures have been used for over two millenia and inorganic fertilizers for over one century with great benefit in increased plant growth and better crop quality (137). However, modern methods of intensive agricultural production have sometimes been accompanied by undesirable effects from fertilizers (39, 60) and the advent of extensive use of inorganic fertilizers on forests (19, 183, 220) warrants a more complete understanding of the consequences of manures and fertilizers on the different components of the soil ecosystem. The soil faunal component comprises a multiplicity of species that have an intricate relationship among themselves, with the soil microflora and with higher plants. Fertilizers and manures change the milieu and the interrelationship among the organisms so that some species are favoured, whereas others are affected adversely. In agricultural soils this might not be serious because tilling, cultivation, use of pesticides and biological activities other than those of animals might be adequate to maintain and even enhance soil fertility and the importance of soil animals might not be very great (116). However, if the soil fauna is reduced or eliminated in the more stable forest soils, the process of soil formation could slow down or stop altogether, with serious consequences to long-term fertility (52). In addition, subtle changes in forest soils, often requiring many years to distinguish (17), are important because of the long crop rotation

and less intense management practices.

Research on the effects of manures and fertilizers on soil fauna, over the past 50 years, has been conducted almost exclusively in Europe and this is reflected in reviews in German by Klapp and Wurmbach (121), Mayer-Krapoll (144) and Müller (157) and in Russian by Lavrov (129). Only brief accounts have been published in English (17, 73, 116, 161, 241). This, coupled with the recent interest in the role of soil fauna as plant pests and in nutrient cycling, have made it important to compile information on the effects of these amendments on soil fauna.

While available data on manures are from arable and grasslands only, fertilizers have been applied to a range of agricultural and forest soils, the latter being mainly acid soils supporting conifers. The results from this range of habitats indicate that these amendments cause varied and complex faunal changes, involving several biotic and abiotic interactions, which produce different responses by the various groups and diverse species within groups. Results for the same animal species may conflict, depending on (a) soil type, (b) cultural practice, (c) plant cover, (d) kind of amendment, (e) combination of amendments, (f) rate of application, and (g) time of sampling since application. Thus, generalizations are often simplistic or may contradict specific examples.

Because of the many different types of manures and fertilizers that have been used and the large number of animal species encountered in the soil, it is impossible to consider separately each animal species and amendment combination. Therefore, this review is presented in two major sections. The first separates some of these variables by dealing with

the response of species, or other low taxonomic units, within six higher taxa to different groupings of manures and fertilizers and under different cultural practices. The second section is concerned with ways in which organic and inorganic fertilizers effect faunal changes and the duration of faunal response. Thus, the latter section attempts to synthesize the information into principles that indicate general ways in which species and populations might change.

FAUNAL RESPONSE TO MANURES AND FERTILIZERS

DIVISIONS AND PROPERTIES OF AMENDMENTS

Inorganic fertilizers are chemical substances that promote plant growth. For this review, these substances are considered in four major categories: (a) single elements, (b) complete fertilizers, which are comprised of various ratios of NPK alone or in combination with other elements, (c) mixed fertilizers, which contain more than one element but are not necessarily complete fertilizers, and (d) nitrogenous fertilizers, some of which may contain elements other than nitrogen, but differ from mixed, in which nitrogen is not necessarily the main component.

Manures, whose chemical composition is not usually specified, are separated into five groups that are likely to contain similar quantities of nutrient elements: (a) farmyard manure, (b) composts, (c) mulches, (d) sewage sludges, and (e) liquid manure (tankage). Besides supplying nutrient to plants and food for soil animals, manures contain their own fauna.

The fauna of manures: Fresh heaps of organic matter contain

very few or no animals but, as the heaps age, there is a succession of animals paralleling the chemical changes during decomposition (149). Typical manure animals are replaced by compost animals which, in turn, are displaced by typical soil fauna (34). In leaf-compost, mites may initially predominate but are later surpassed by collembolans (73). Among the collembolans, certain species are shown to be regularly eliminated by aging of the compost (155). The first inhabitants were Hypogastrura assimilis (Krausbauer, 1898) and Hypogastrura denticulata (Bagnall, 1941), followed by Friesea mirabilis (Tullberg, 1871) and Onychiurus fimatus Gisin, 1952 . "Ripe" compost contained Proisotoma minuta (Tullberg, 1871 and Proisotoma thermophila (Axelson, 1900).

In compost-earth, the animals increased to a maximum at the start of decomposition then decreased markedly, unless fresh decomposable material was added (216). In 1 kg of air-dry young compost, 416,000 animals declined to 32,000, 26,000 and 4,000 in 6 months, 2 years and 4 years, respectively. There was a corresponding decrease in the number of taxa, from 17 at the beginning to three (nematodes, mites and collembolans) 4 years later. Stöckli (216) concluded that well-rotted compost, 3 years old, may not contain a greater metazoic fauna than grassland or arable soils.

Tischler (223) pointed out that the number of species in manure might be small but the number of individuals and biomass was greater than in the soil. Using data from Gunhold (84) and Graff (79), Tishler (op. cit.) derived the following figures per m^2 for a 10-cm depth: millions of nematodes, 300,000 mites, 150,000 enchytraeids, 130,000 collembolans,

30,000 insects and 300 earthworms. Mrohs (155) listed the order of abundance in compost as mites, collembolans, the bandling earthworm, Eisenia foetida (Savigny, 1826) and enchytraeids. Other important groups include dung-fly larvae and staphylinid beetles (116). Therefore, the number of individuals and species of a particular group that would be added to a field by manuring would depend on the nature and age of the material, and its degree of decomposition.

The succession of species also continues under field conditions. Two or 3 weeks after manure application, the manure population begins to decrease, but the total faunal counts usually remain higher than in undunged fields (132).

NEMATODA

Manures

Farmyard manure: Although total nematode populations tend to increase immediately following manuring (Table 1), saprozoic and plant-parasitic groups respond differently (21, 77, 200, 245). Various types of organic amendments are known to suppress the rate of infection or reproduction of plant-parasitic genera such as Ditylenchus, Aphelenchus (229), Tylenchorhynchus, Hirschmaniella (177, 229), Pratylenchus (148, 171, 212, 229), Heterodera (171), Meloidogyne (45, 171, 177, 211) and Rotylenchus (200). In contrast, lower numbers of Pratylenchus in unmanured as opposed to manured plots were attributed to poor root growth (41). Heald and Burton (88) also observed that in unmanured plots where grass grew poorly, the sedentary, pseudo-root-knot nematode, Hypsoperine graminis

Sledge and Golden, 1965 , was suppressed by the migratory, sting nematode, Belonolaimus longicaudatus Rau, 1958 , which probably prevented the pseudo-root-knot nematode from multiplying rapidly because of competition for food.

The non-parasitic nematode genera, Acrobeles and Diplogaster, may be reduced by dunging (200, 229) but, in general, manuring increases saprophages, bacterial feeders and predators, such as Acrobeles, Rhabditis (200), Aphelenchoides, Cephalobus, Discolaimus, Dorylaimus and Mononchus (133, 177).

The mechanism for reduction of certain nematode species by organic amendments is not fully understood, but involves numerous factors. Perhaps physiological changes in cover plants make them more resistant to attack (127). Manures may also contain organisms antagonistic to parasitic nematodes (45) or chemicals produced during degradation may be the controlling agents (224, 231). The chemicals are probably specific to the type of organic amendment (200) and may act through increased osmotic pressure of the soil solution and through toxic effects (112, 174, 211). Evidently, organically amended soils create conditions favourable for the increase of predatory nematodes (127, 165), and are also usually associate with the more efficient nematode-trapping fungi, Dactylella ellipsospora Grove, 1886 and Arthrobotrys dactyloides Drechsler, 1937 (141). According to Wallace (cf. Laan, 127, page 125), emergence of beet eelworm larvae from cysts show some correlation between rate of emergence and soil oxygen-consumption, the latter being associated with the amount of organic matter, and suggest a competition for oxygen between nematodes

and soil microorganisms.

Nematode parasites and predators include viruses, bacteria, protozoans, turbellarians, tardigrades, enchytraeids and arthropods, especially mites, collembolans, symphylids, centipedes and staphylinid beetles (25, 233, 240). Many of these groups increase following manuring. Microphagous nematodes also rapidly reproduce on the bacteria associated with decomposition; thus, parasitism and predation of both phytonematodes and free-living forms apparently result in a proportionally greater reduction of plant-parasitic species (133).

Liquid manure: Liquid manure, applied at the rate of 50 m^3/ha three times a year, did not reduce nematode populations, but it changed the qualitative composition of the fauna (86). Gunhold (85) found that applying liquid manure for 22 years to grasslands at the rate of 70 m^3/ha brought about a 2- to 3-fold decrease in the total soil population and modified the faunal composition. This he felt would lead to soil damage and yield losses if other kinds of fertilizers were not also used. Like Franz (64) and Gusenleitner (86), he noted that liquid manured plots favoured decomposer-nematodes like Dorylaimus bastiani Butschli, 1873 Odontolaimus chlorurus de Man, 1880 , detritous feeders in the genus Rhabditis and the stylet-bearing (plant-parasitic) genera Tylenchus, Rotylenchus, Pratylenchus and Aphelenchoides.

Fertilizers

Mixed fertilizers: In both agricultural and forest soils, most fertilizers tend to increase total nematode populations (Table 2), but

saprophagous and plant-parasitic species behave differently (106, 245, 246). Various fertilizers (NPKCa, PKCa, NKCa, NPK, NPCa) applied at different rates in a pine stand did not increase total nematode population, but semisaprophagous species in the genera Panagrolaimus, Cephalobus, Eucephalobus, Teratocephalus, Plectus, Wilsonema and Monhystera increased in numbers, and plant-parasitic and semi-parasitic species, especially in Tylenchus, Ditylenchus and Aphelenchoides, decreased (15). Such decreases in plant-parasitic species following fertilization is not related to increased plant growth, although the opposite is possible. For example, low numbers of Pratylenchus in unfertilized plots, as opposed to fertilized plots, were attributed to poor growing plants with small root systems (41), suggesting that a limited quantity of fertilizer is required for host plants to support maximum nematode populations (10, 78, 88).

Plant-parasitic nematode reproduction and development rates are influenced by metabolites that change with host nutrition and growth (152). Thus, there is a differential stimulation of plant-parasitic species by fertilization. With a factorial NPK experiment, numbers of Xiphinema americanum (Cobb, 1913) and Pratylenchus penetrans (Cobb, 1917) were significantly lower under trees receiving high rates of potassium (119). Since phosphorus tended to be more residual than nitrogen and potassium, continuous use of a complete fertilizer at low rates of application shifted cherry tree nutrition toward a high phosphorus low potassium status that favoured increases in populations of X. americanum and P. penetrans (120). Both these species also increased as phosphorus and potassium alone increased,

as a result of increased tree growth, but X. americanum decreased again as leaf potassium climbed to 2.21%. Helicotylenchus dihystra (Steiner, 1945) Sher, 1961 and Tylenchorhynchus sp. also increased in response to higher plant vigour resulting from increased rates of potassium.

Although the relationship between plant nutrient levels and nematode attack is not fully understood (10), potash content is apparently inversely related to nematode pathogenicity (201, 212). Unfortunately, the significance of plant nutrition in nematode control is difficult to interpret, because superimposed on these nutritional relationships are the complex reciprocal effects of plant-parasitic nematodes on host nutrition (196, 218, 219).

Nitrogenous fertilizers: These normally stimulate plant growth and increase indirectly some plant-parasitic nematodes; but depending on form of nitrogen and rate of application, they may also directly effect soil nematodes. Some forms are attracted by ammonium (115), but generally nitrogenous fertilizers appear to be inimical to plant-parasitic species. Urea, for example, at 1,000, 3,000 and 5,000 ppm reduced Tylenchulus semipenetrans Cobb, 1913 populations by 81.6, 97.6 and 99.9%, respectively (172). Liquid ammonia also exhibited nematicidal properties (198) with a tendency to reduce predaceous forms. Eno et al. (57) found that Mononchus and plant-parasitic genera such as Pratylenchus, Belonolaimus, Xiphinema and Hoplolaimus were killed in the ammonia retention zone, with subsequent recolonization favouring saprophytic species.

Walker (231, 232) investigated the action of nitrogenous compounds that reduced populations of Pratylenchus penetrans. Similar

decreases in nematode populations following organic amendments have been attributed to: increased predators, nematode trapping and predaceous fungi, toxins from fungi and higher plants or both, and changes in soil-solution osmotic pressure, but Walker (232) concluded that ammonia and possibly nitrates produced during transformations of nitrogenous fertilizers were among the principal compounds responsible for the decrease of plant-parasitic nematodes. He also recognized that the direct or indirect influence of pH, ca^{++} ions, moisture, temperature, and other factors of microbial activity affected nitrification and nematode populations. For example, a combination of dextrose and ammonium nitrate reduced Meloidogyne hapla Chitwood, 1949 by stimulating the action of the nematode-trapping Hyphomycete, Arthrobotrys oligospora Fresenius, 1852 (170). Excessive nitrogenous fertilizer, however, induced a high infection rate of Aphelenchoides besseyi Christie, 1942 in rice paddies (104).

Calcium: The addition of 0.84 to 10 t CaO/ha to forest humus gave a statistically significant 25 to 100% increase in nematode population (13, 14). The species remained essentially the same, but the ratio of various trophic groups changed, with bacteria-feeding species being favoured. Parasitic and saprophagous species decreased, especially among the genera Cephalobus, Tylenchus, Aphelenchoides, Plectus, Monhyster and Rhabditis. However, pollution by sulphur dioxide, which decreased tree stand, and by excessive lime, which raised pH from 3.7 to 7, significantly reduced nematode numbers and altered species composition, favouring saprophagous and predatory species (16).

Such decreases following lime application are probably related to the depletion of organic layers, which Franz and Loub (70) showed decreased by a third of the original quantity within 5 years following liming and other fertilizer treatments.

OLIGOCHAETA

Manures

Most annelid worms, including aquatic groups, terrestrial earthworms and potworms (Enchytraeidae) belong to the Oligochaeta. In this review, the earthworms and enchytraeids are discussed separately. According to Edwards and Lofty (54), the Megascolecidae and Lumbricidae, in terms of number and human welfare, are the most important terrestrial oligochaete families and most of the earthworm species mentioned below are lumbricid worms.

Earthworms

Farmyard manure: Lumbricid worms are among the soil fauna that show the greatest increases to organic amendments (Table 1). An increase in numbers and biomass occurred in manured plots as opposed to unmanured controls (243), and in plots receiving 14 t/ha farmyard manure and 0.75 t/ha guano once every 4 years; the population was 3 to 4 times greater than in unmanured plots (202). Farmyard manure benefits earthworms directly by providing food and indirectly by promoting plant growth, which increases soil organic residue (46). Worms, selective in their feeding habits, prefer dung or succulent herbaceous materials, especially those high in nitrogen and sugar content, to woody or fibrous parts of

plants, but they will eat almost any form of organic matter (83). Satchell (204) suggested that favourable responses to organic amendments were related to available protein in the food, since Evans and Guild (59) found that the amount and type of organic matter influenced cocoon production in Allolobophora chlorotica (Savigny, 1826) and Lumbricus castaneus (Savigny, 1826). Also, Barley (11) showed that Allolobophora caliginosa (Savigny, 1826) grew faster when fed a nitrogen-rich diet.

Species that respond well to manure include: A. caliginosa, Allolobophora nocturna (Evans, 1946), L. castaneus, Octolasium cyaneum (Savigny, 1826) (202), Allolobophora rosea (Savigny, 1826) (27, 209) and Lumbricus terrestris L. (27, 54). E. foetida appears to be essentially a dung and compost species (130, 158) and does not survive in the field, as Doeksen (46), who surveyed grasslands and arable soil in Holland, did not find it, although Lumbricus rubellus Hoffmeister, 1843 and A. caliginosa were frequently encountered.

Mulches: Grass and other forms of organic mulches also increase earthworm activity (81, 93, 126, 159). Graff (80) estimated that on straw covered plots A. caliginosa averaged, over 3 years, 138 specimens weighing 35 g as opposed to 92 weighing 22 g on controls.

Enchytraeids

Various farmyard manures increased enchytraeid numbers by providing food and better moisture conditions during dry periods (207). Five years after annual application of stable manure at 2 t/ha, treated plots contained 50% more enchytraeids than controls (205), with increases primarily in the top 10 cm of the soil (206, 207). Under agricultural

cropping, a single dose of manure seemed to affect beneficially enchytraeid populations for 3 to 10 years (64, 100, 118).

Fertilizers

Earthworms

Mixed fertilizers: Seemingly contradictory observations on the effects of fertilizers on earthworms (12, 227) result from not specifying the type of fertilizer applied or the earthworm species affected. Sulphates and phosphates used alone may be detrimental to many earthworm species, but other fertilizers generally favour earthworm populations (Table 2). Other data demonstrating population increases include those by Bilger (20), Brauns (28), Franz (66), Ronde (191, 192) and Ronde et al. (193). Fertilizer effects may be direct through chemical changes in the soil or indirect by increasing plant production.

Many authors (46, 203, 210, 239, 243) have noted an increase in earthworms as a result of increased production of agricultural crops following fertilization. Improvement in herbage composition following fertilization also influences earthworms, as from coarse grass and heather plants to pasture grass and legumes, which provide a richer protein diet (113, 189, 210). Guild (82) observed that Bimastos eiseni (Levinsen, 1884) Dendrobaena rubida (Savigny, 1826), Dendrobaena octaedra (Savigny, 1826), L. castaneus and L. rubellus, present under acid heather conditions, were dominated by A. caliginose, A. chlorotica, Allolobophora longa Ude, 1885 , Eisenia rosea (Savigny, 1826), L. terrestris and O. cyaneum in fertilized plots. On grazed pastures receiving fertilizers, worm increases corresponded

to more dung being returned to the soil (210, 239).

Nitrogenous fertilizers: Richardson (185) found fewer worms on plots receiving nitrate of soda than on unfertilized grassland plots, but the bulk of evidence indicates that nitrogenous fertilizers, which do not acidify the soil (e.g. nitro-chalk, nitrate of soda, calcium nitrate), increase earthworm populations in agricultural soils (20, 58, 167, 239) and forest soils (18, 69, 70). Jacob (107) and Jacob and Wiegand (108) showed that following application of different forms of nitrogenous fertilizers, there were 128 worms per m^2 in controls as opposed to 176 per m^2 in fertilized plots. Biomass also increased from 274 to 377 kg/ha for controls and nitrogen-fertilized plots, respectively. Heath (89) also recognized that numbers alone may give an imprecise estimate of change and demonstrated that there was a linear correlation between the amount of nitrogen used and the weight of earthworms in the soil.

Fertilizer salts and anhydrous ammonia are lethal when applied in contact with living worms, but applied fertilizers directly contact only a very small part of the soil habitat occupied by earthworms (169). Thus, Zajonc (247), studying the effects of various nitrogen levels on earthworm populations of a prairie soil, found that 300 kg N/ha did not effectively change the total population biomass, but there was a reduction in surface-dwelling species such as Allolobophora antipae typica (Michaelsen, 1891) and Allolobophora tuberculata Eisen, 1873 and an increase in deep-dwelling species, such as A. rosea, L. terrestris and Dendrobaena platyura (Fitzinger, 1833).

Sulphates: Ammonium sulphate seems to be antagonistic to

earthworms (43, 54, 125) and discourages cocoon production (188). Jefferson (109) observed that A. caliginosa and L. rubellus could survive ammonium sulphate-treated plots, but Slater (213) showed that continuous use of this fertilizer decimated earthworm populations, and recommended 280 kg/ha for controlling earthworms on neutral or acid soils.

Phosphates: The effect of superphosphates on earthworms is not clear. Doerell (49) stated that superphosphates were beneficial to earthworms in arable soils; Sears and Evans (210) were unable to detect a detrimental effect on them in grasslands 3 years after application; however, Escritt and Arthur (58) contended that superphosphate discouraged earthworm activity.

The deleterious effects of phosphates and sulphates on earthworms depend on soil type and application rate (8), and are generally attributed to the acidifying nature of these fertilizers (109, 202, 213). pH is undoubtedly important, but other factors might be involved. For instance, Khan (117) studied the effects of different rates of ammonium sulphate mixed with saltish "Kallar" soils on Pheretima posthuma (L.) (Vaill., 1868) and E. foetida. He found that worms died in unfertilized soil if the pH was above 8.3, and in fertilized soils receiving 1800 kg ammonium sulphate per hectare - a rate not excessive under certain agricultural conditions (143) - even though the pH of the mixture was 7.5. In ordinary "Kallar" soils plus manure at pH 8.3, the worms remained healthy. Alexander's (4) suggested pathway for the reduction of sulphates in soils probably explains how, especially under wet conditions, sulphates

and phosphates, which contain an appreciable amount of calcium sulphate, could be reduced to hydrogen sulphide. This gas is toxic to many soil animals (104, 125, 153). L. terrestris was shown to be sensitive to 2% hydrogen sulphide by Doeksen (47), who theorized that the iron atom in the worm's haemoglobin was perhaps activated in an irreversible process similar to hydrogen cyanide and carbon monoxide poisoning.

Calcium: Liming generally benefits earthworms in agricultural (54, 71, 189, 214) and forest soils (26, 61, 142). Population biomass increased from 36 to 123 kg/ha in pastures for controls and lime plus superphosphate-treated plots, respectively (113). Similar high increases have been obtained for forest soils. Franz (67) found a 3- to 10-fold increase in L. rubellus following calcium application, and Kleinschmit (123), who studied different rates of liming on a population comprising D. octaedra, E. foetida, L. castaneus and L. rubellus, observed increases in both numbers and biomass. Unlimed plots contained no worms, whereas 3, 6 and 11 t CaO/ha gave populations of 140, 455 and 172 thousand worms per hectare, respectively. Corresponding biomass for these three rates of liming were 4.4, 25 and 10 kg/ha.

Increases in earthworm activity is sometimes effected by better plant growth from liming (20, 82, 110). Liming also encourages acid intolerant plants, whose litter tends to be richer in bases (42). These bases may have assisted in the decomposition of organic matter, making it a more suitable food (58), but Edwards and Lofty (54) doubted this conclusion as earthworms seemed to be primary litter breakdown organisms.

Calcium is excreted from calciferous glands and plays an

important role in earthworm metabolism (204). A minimum supply of calcium ions is essential in maintaining good water relationships between the animal and its environment (128). Perhaps this is a factor that excludes some earthworms from acid soils (24, 75). Many species seem to do best in neutral soils, but there is a range of responses from pH 4 for acid tolerant species such as B. eiseni and D. octaedra to pH 9 for alkaline tolerant species such as Hyperiodrilus africanus Beddard, 1891 (54); thus, each biotype is characterized by a specific earthworm fauna (5).

Although much has been written about soil reaction and earthworm distribution, it is still not clear whether it is the acidity itself (hydrogen ion concentration) or the low content of available calcium that is unfavourable to the worms. On the one hand, 10 parts calcium per 10,000 parts soil was necessary to maintain health and a normal rate of reproduction in A. caliginosa, though L. rubellus and O. cyaneum appeared less sensitive to lime deficiency (163). A linear relationship existed between earthworm population and exchangeable calcium, with Allolobophora terrestris (Savigny, 1826), A. caliginosa and Lumbricus spp. responding critically between 3 to 10 milliequivalents per 100 grams of soil (110). On the other hand, some earthworm species were sensitive to hydrogen ion concentration (202), and species normally found in mull soils were absent from calcium-deficient podozols of Rhum, whose pH, because of high magnesium content, was between 5.0 and 7.0 (204). Satchell (204) concluded that calcium may limit earthworm population directly but, since mull species die on the surface of very acid soils without ever ingesting any soil, their immediate absence from mor-type soils was probably not

due to nutrition, but to their sensory response to acidity.

Potassium: Evidence that potassium directly affects earthworms is lacking; however, low potash levels may restrict plant growth and ultimately limit the amount of food available to worms (163).

Enchytraeids

Complete fertilizers: Although these worms may benefit from fertilization (62, 72), they appear to be very sensitive to some formulations (Table 2). During the first year following the application of a complete fertilizer at the rate of 800 kg/ha, enchytraeid populations decreased by 70% of controls, then they recovered and from 3 to 5 years after fertilization, enchytraeids were the only soil faunal group to show a clear increase (80%) over controls (103).

Nitrogenous fertilizers: Urea fertilization also causes a temporary decline in enchytraeid numbers (Marshall, unpub.) but not all species are adversely affected. Three years following application of urea at the rate of 160 kg/ha, Enchytraeus buchholzi Vejdovsky, 1879 , Mesenchytraeus flavus (Levinsen, 1884) and Mesenchytraeus pelicensis Issel, 1905 increased over controls but Cognettia sphagnetorum (Vejdovsky, 1877), which Abrahamsen (3) regarded as a dominant species in northern European forest soils, dramatically declined and remained far below controls for the 4-year observation period (2). The reduction of C. sphagnetorum occurred particularly in the humus and resulted in a higher ratio of specimens in mineral to humus in the fertilized plots as opposed to unfertilized plots.

Calcium: Mayer-Krapoll (144) noted a reduction of enchytraeids

under pine fertilized with calcium, which presumably caused a depletion of the raw humus and thus food and living space of the worms.

MYRIAPODA

Manures

This group of arthropods consists of the Pauropoda, Symphyla, Chilopoda and Diplopoda. All four classes seem to benefit from manuring (132, 180). Herbke (90) demonstrated that diplopod population densities were 180% higher in treated plots than controls, even 10 years after the last manure application. Greater species diversity was also evident in manured plots: Polydesmus germanicus Verhoeff, 1896 and Polydesmus denticulus Koch, 1847 were not influenced by manure, but Boreoiulus tenuis Bigler, 1913 and Cylindroiulus teutonicus (Pocock, 1900) increased in numbers, and Brachydesmus superus Latzel, 1884, Brachyiulus littoralis Verhoeff, 1898, Blaniulus guttulatus (Bosc, 1791) and Ophiodemus albonanus (Latzel, 1895) were restricted essentially to manured plots. Chilopods (Geophilidae) were more numerous on manured plots, but the symphilids showed no clear reaction.

Fertilizers

Mixed fertilizers: Myriapods seem to benefit more from fertilization of forest than agricultural soils (190, 225) (Table 2). Since millipeds are primarily saprophages, their increase is usually associated with increased crop yield. However, Herbke (90) found that P. germanicus and symphylans were somewhat correlated with potassium and B. guttulatus showed a strong correlation with calcium.

Calcium: Liming forest soils did not strongly affect myriapod population (14). Since chilopods are mainly carnivors, their increase following liming (190) is probably related to increases in microarthropods on which these myriapods feed.

INSECTA

Manures

Soil contains an abundant and diverse insect fauna, with representatives from most Orders. Some of these are unimportant members of the soil ecosystem because of sporadic distribution and low densities; others are important only in some regions of the world; for example, the mainly tropical Isoptera (236). However, the Collembola or springtails are ubiquitous and usually abundant; therefore, they are treated separately below.

Collembolans

Farmyard manure: Although some contradictory evidence exists, manures are generally very effective in increasing soil collembola (35). Holler-Land (98) compared total collembolan population in agricultural fields, half of which received fertilizers alone, the remainder inorganic fertilizers plus manure. In fields under truck crops (potatoes, turnips, cabbage, etc.), the annual average number in the unmanured plots was only half that in the manured plots 3 years after the last application of manure. A less spectacular increase in fields under legumes was attributed to various cultural practices associated with crop rotation, which are known to affect the distribution and generally reduce the abundance

of soil fauna (e.g. 7, 53, 116, 180, 223).

When farmyard manure is added to the field it carries a rich hemiedaphic collembolan population that may persist for a short while. Morris (151) observed that in dunged plots, Anurida granaria (Nicolet, 1847) and Onychiurus fimetarius (L.) were the dominant species, whereas in undunged plots, it was Onychiurus armatus (Tullberg, 1869). Hemiedaphic species of decomposing manure are, however, eventually replaced by true euedaphic forms (63).

Gisin (76) documented these changes over a 2-year period for farmyard manure added to soil. Essentially, dung species such as Proisotoma pontica (Stach, 1947), Hypogastrura manubrialis (Tullberg, 1869) and Xenylla welchi (Folsom,1916) diminished during the first year; Friesea claviseta (Axelson,1900) diminished slowly during the second year, while Tullbergia krausbaueri (Börner, 1901) and Isotoma notabilis (Schäffer, 1896)increased. Gisin concluded that farmyard manure temporarily stimulated certain Collembola but did not depress true soil forms such as Isotomiella minor (Schäffer, 1896) O. armatus, Onychiurus campatus (Gisin, 1952), Proisotoma parvula (Stach, 1922), Oncopodura crassicornis (Shoebotham, 1911), Pseudosinella alba (Packard, 1873) and Neelus minimus (Willem, 1900). Höller-Land confirmed that T. krausbaueri and I. notabilis were active manure decomposers and added to these Tullbergia ramicuspis (Gisin, 1953), I. minor, Folsomia fimetaria (L.) and N. minimus as species that respond well to manure.

Mulches: Grass mulch also stimulated collembolan populations (96). The annual population density in 35 cm soil layer on mulched plots

was 76,000 as opposed to 26,000 per m^2 on plots where hay cover was regularly removed. Atlavinyté (6) incorporated straw at the rate of 17 t/ha in potted soil, and the collembolan population, which was less than 20 individuals at the beginning of the experiment, increased to over 1,000 individuals per pot 6 months later. Pots with numerous earthworms also supported the highest collembolan densities. Straw decomposition, like that of compost and dung, is associated with collembolan succession. This might be related to changes in the microfungi which serve as food for many collembolans (162).

Sewage sludge: The collembolan population in soil treated with sewage sludge increased eight-fold a few months after application, but returned to pretreatment levels within a year (97). The species succession was somewhat similar to that in decomposing manure. H. denticulata and Isotoma olivacea (Tullberg, 1871), early colonizers of fresh sludge, were gradually replaced by I. notabilis and T. krausbaueri, followed by I. minor in the late stages of decomposition.

Liquid manure: Applied at the rate of 50 m^3/ha three times per year, liquid manure reduced collembolan populations 30% 1 month after application, but the population usually returned to pretreatment levels within 2 years (86). However, the continuous use of liquid manure permanently modified the qualitative composition of the fauna. Gunhold (85) found only manure-loving forms like Tullbergia quadrispina (Börner, 1901), O. fimetarius, Folsomia quadrioculata (Tullberg, 1871) and Lepidocyrtus cyaneus (Tullberg, 1871) and the water-loving Isotomurus palustris (Müller, 1776) in plots that received liquid manure for 22 years.

Other Insects

Other insects, particularly Coleoptera, Hymenoptera, Diptera and Thysanoptera (180), usually increase following organic amendments (Table 1), and Diptera that originate with the manure might greatly contribute to the increases observed in the field (132). Some organic substances are more effective than others. For example, Phyllophaga and other Coleoptera were stimulated more by stable and green manure than by straw (178, 244).

Fertilizers

Collembolans

Mixed fertilizers: Table 2 shows that in both agricultural and forestry situations springtails generally benefit from fertilization. The increases are often accompanied by species changes. For example, high collembolan populations following "Wichtel" complete fertilization of meadows were mainly composed of five species: Folsomia multiseta Stach, 1947 , I. notabilis, I. minor, Brachystomella parvula (Schäffer, 1896) and L. cyaneus (132). On the other hand, the petro-xerophyle, Schoetella ununguiculata (Tullberg, 1869), was present only in unfertilized plots.

Based on collembolan distribution in agricultural plots that received different fertilizer treatments, Höller-Land (98) theorized about expected species response. Thus, of 13 species listed, none should be reduced by calcium and phosphorus; O. armatus should be adversely affected by complete fertilizer and excessive potassium, and T. ramicuspis, T. quadrispina, T. krausbaueri, O. armatus, I. notabilis and N. minimus from excessive application of nitrogen.

Nitrogenous fertilizers: Most workers have recorded springtail increases in forest soils from various nitrogenous formulations (87, 144, 190-193, 156, 225). Even among the nitrogenous formulations there are differential responses; for instance, Weetman et al. (242) recorded a 0.9-, 1.8- and 2.4-fold increase over controls in springtail population, 2 years after fertilizing a black spruce stand, with 448 kg N/ha of ammonium nitrate, calcium nitrate and urea, respectively.

Where decreases have occurred, they do not seem to be related to type of fertilizer, rate of fertilizer or time since application. Reduction from urea was non-significant (18) and those from other nitrogenous fertilizers accompanied by calcium (70, 144) were probably related to the depletion of organic matter. Population fluctuations over time (102) are to be expected because, like other soil animals, collembolan species are regulated by many factors. A decrease in predators and competition groups might be important (132). Although some species tolerate acid soils (35), the general tolerance range is pH 6 to 7.8 (31). Thus, when other factors are not limiting, fertilizers that neutralize soil reaction can be expected to favour directly collembolans. Fertilizers also alter the micro- and macroflora and affect the quality and quantity of collembolan food (98). For example, maximum increases in collembolan populations following phosphate fertilization were correlated with two factors: pH about 6.5 and a level of phosphorus that produced the best grass sward (230). Other factors interact to determine collembolan abundance, and it is difficult to distinguish the effect of any one of these factors from the others (164).

Phosphorus: Collembolan populations have generally increased following application of phosphorus alone or in combination with other elements (87, 144, 230). These increases are probably less related to the phosphorus *per se* and more influenced by increased fungal (190) and plant growth (230).

Potassium: Carey *et al.* (33) noted a 5% decrease in collembolan population from controls 5 years after application of 448 kg K/ha as potassium chloride to a red pine plantation.

Calcium: Liming agricultural soils generally increased collembolan populations (53, 64). Forest soils show no such clear pattern. In numerous situations, the population seemed unaffected (14, 67, 70, 87, 144, 190, 193), while in other situations, these same authors have recorded increases. Positive responses were unrelated to rate of application and to forest or soil type, but occurred more commonly from 2 to 4 years after application. For example, Ronde (190) observed a two-fold increase in Collembola and species composition did not change 2 years following application of 2.3 t CaO/ha. The major species that occurred on both limed and unlimed plots were: *F. quadrioculata*, *Hypogastrura armata* (Nicolet 1841), *I. notabilis*, *I. minor* and *O. armatus*. In contrast, others (14,70,142, 144,190) noted statistically non-significant decreases in collembolan population following liming. Such decreases may suggest a future trend, especially where the store of litter is being depleted.

Other Insects

Mixed fertilizers: Insects other than collembolans also usually increase following fertilization (Table 2), but data have been reported

mainly by Orders, within which species are expected to behave differently. Urea, applied at the rate of 448 kg N/ha increased the density of dipterous larvae (particularly cecidomyidae)(242), but ants, normally numerous on unfertilized plots, were reduced by complete "Wichtel" fertilizer (132). Two ant species, representing most of the population, showed clear differences: Lasius flavus Mayer, 1886 was reduced but remained in the population, whereas Myrmica scabrinodis Mylander, 1846, which prefers stony ground with sparse vegetation, was decimated as a result of luxuriant plant growth. Lasius niger L. was not affected by 200 and 410 kg N/ha as ammonium sulphate (105), nor was the grass grub, Odontria sp., by 325 kg/ha superphosphate alone or with 62 kg CaO/ha(210).

Calcium: The relationship between liming and insect populations is sketchy. Although many families in the Coleoptera, including carabids, scarabids and staphylinids, seem unaffected (14) or increase initially following liming (178), the Japanese beetle grub, Popillia japonica Newman, 1841 behaved differently. Polivka (176) found that this species was 2 to 10 times more abundant in unlimed than in limed plots receiving 1.2 to 2.6 t CaO/ha.

ACARINA

Manures

Farmyard manure: Primavesi and Côvolo (178) suggested that mites did not respond favourably to manure because of their aversion to nitrogen, a view opposed by others. In a field with grass, grain and potato rotation, an average of 6,138 and 625 mites per m^2 occurred for

manured and unmanured plots, respectively (118), and with sugar beet and grain rotation, the annual average was eight times greater for manured plots (207). The latter increase was unrelated to kind (fresh, old or composted) and frequency of manure applied at 2 t/ha once a year or 6 t/ha applied once every 3 years.

Different acarine groups predominate at different times following manuring, with increases observed by Sauerlandt and Marzusch-Trappmann (206), 5 years after application, being due mainly to Trombidiformes (or Prostigmata). Also, Höller (95) found that 3½ years after manuring truck-crop fields, the Mesostigmata were twice as numerous in manured plots compared to unmanured controls. Favoured genera included Ologamasus, Hypoaspis, Pachylaelaps, Gamasellus and Macrocheles. Manure was seemingly of no special advantage to Podociniae, Neoparasitidae or Veigaia. In contrast to Mesostigmata, the Cryptostigmata (or oribatids) decreased slightly in manured plots. Hypochthonius luteus Oudemans, 1917, Heminothrus sp., Amerobelba decedens Berlse, 1908, Tectocepheus velatus (Michael, 1880), Oppia minus (Paoli, 1908), Ceratozetes gracilis (Michael, 1884) and Zygoribatula terricola Hammen, 1952 decreased or were unaffected, whereas Brachychthonius brevis Berlese, 1910, Eniochthonius grandjeani Hammen, 1952 and Oppia clavipectinata (Michael, 1885) were probably stimulated by manure, as large samples of these species were found associated with manure balls. Various members of the Prostigmata reacted differently. In manured plots, Nanorchestes arboriger (Berlese, 1905), Alicorhagia fragilis Berlese, 1910, Coccorhagidia, Rhagidia, Eupodes, Protereunetes and Pyemotidae increased, whereas Speleorchestes

poduroides Hirst, 1917 and Tarsonemidae decreased.

Increases in the Mesostigmata and Prostigmata observed by Höller (95) from manure and in Parholaspulus alstoni Evans, 1956 , Eugamasus sp. and Pachylaelaps sp. by Heungens (92) from an application of malt germ in pot cultures, were probably due to an indirect amendment effect. These mesostigmatid genera are primarily predators on collembola and other microarthropods (114, 235) that usually increase following manuring. Also, Höller (95) considered that increases in small Prostigmata like Alicorhagia and Protereunetes were related to increases in microbial populations stimulated by sulfur in the manure.

Mulches: Crop residues and other mulches favour acarine populations (9), particularly the oribatids. The annual population density of mites in a 35 cm soil layer on control plots was 23,000 compared to 44,000 per m^2 on mulched plots (96). In pot cultures with straw incorporated at the rate of 17 t/ha, mite densities increased 10 times more than in pots without straw (6). Increases were highest in the middle of humification (6 months following straw incorporation) and dropped to equal controls 1 year after the start of the experiment.

Sewage sludge: Höller (94) investigated the acarine succession in garden soil treated with sewage sludge. Mites were initially completely eliminated but they later recolonized the soil, and reached normal soil populations after 4 months. Two distinct faunal stages existed during sludge decomposition: the first was characterized by Hypoaspis spp. and Pyemotidae, and the second by Uropodina. The astigmatid mite, Caloglyphus mycophagus (Mégnin, 1874), was also abundant when lime was added to the

sludge. Oribatids, however, were absent and seemed to occupy a subordinate position during the decomposition of organic matter (92, 179, 206, 223).

Liquid manure: Applied at the rate of 50 m^3/ha three times a year, liquid manure reduced mite populations 50% 1 month after application, but the population usually returned to pretreatment levels within 2 years (86). However, continuous use of liquid manure permanently modified the faunal composition (85). Mesostigmatid mites were decimated and only moisture-loving cryptostigmata, such as Scheloribates laevigatus (C.L. Koch, 1836) and Peloptulus phaeonotus (C.L. Koch, 1841), were regularly found in large numbers in manured plots.

Fertilizers

Mixed fertilizers: Most authors have reported increases in acarine population following fertilization under agricultural and forestry conditions (Table 2). Why this occurs is not always clear but seems primarily related to changes in food. Höller (95) studied the effects of various fertilizer combinations under rotational crops and was unable to determine the factors responsible for acarine decline in some fertilizer plots. For lucerne plots, the elimination of phosphorus from the treatments resulted in poor plant growth and a corresponding diminution of the acarine fauna from 34,250 the first year to 20,500 per m^2 during the third year of continuous lucerne cultivation. He listed Rhodacaridae, Uropoda, Nanorchestes, Ceratozetes, Heminothrus, Oppia and Tectocepheus as phosphorus-requiring mites because they were absent from the 3-year-old lucerne fields, and Tyrophagus dimidiatus (Hermann, 1804) as nitrogen-requiring because of its

abundance on 3-year-old lucerne plots. Höller, however, recognized that other ecological factors might be responsible for the reduction and distribution of the mites.

Nitrogenous fertilizers: Although most of these fertilizers increased mite populations in agricultural (156) and in forest soils (64, 144, 190, 191, 192, 225), different formulations effect different response For example, Weetman et al. (242) recorded a 1.9-, 2.4- and 6.7-fold increase in mite population over controls 2 years after fertilizing a black spruce stand, from 448 kg N/ha of ammonium nitrate, calcium nitrate and urea, respectively. Four months after application of 224 kg N/ha as urea, the species composition remained constant, but the relative abundance of certain orders and species of mites changed (18). There was a 2- and 3-fold increase in Mesostigmata and Astigmata, respectively, over the control; the Cryptostigmata decreased slightly in the fertilized plots. Saprolaelaps sp., Conchogneta dalecarlica (Forsslund, 1947) and Tectocepheus velatus (Michael, 1880), dominant (relative abundance $\geq$ 50%) in control plots, became influent (relative abundance 2-5%). Conversely, a rare Iphidozerc species became dominant in urea-treated plots.

With fertilizers, such as manures, the Oribatei tend to respond less rapidly than the other acarine Orders. This is probably because of their long life cycle and saprophagous feeding habits, whereas the Mesostigmata and Prostigmata are primarily predators with relatively shor periods between generations. The Astigmata are mainly saprophages with short life cycles and, like the Mesostigmata and Prostigmata, could quickly take advantage of favourable conditions induced by fertilization.

Huhta et al. (103) measured fluctuations in mite populations over a 5-year period following the application of a complete "Y forest fertilizer" to forest soils in Finland. Oribatids increased slowly during the first 3 years, perhaps from increased litter fall, then dropped off to equal the control. Mesostigmata and Prostigmata, on the other hand, oscillated about the control during the first 3 years, somewhat parallelling the collembolan population on which these predatory mites might have been feeding.

Decreases in mite populations have been recorded from gaseous ammonia (66) and other forms of fertilizers accompanied by calcium (70, 132). Ammonia is toxic to mites (153) and the neutralizing effect of the calcium could have sufficiently altered the microflora to affect adversely the Oribatei, the dominant acarine group in most soils. Acid-forming fertilizers; for example, ammonium sulphate, which presumably encourage fungal growth, seem less detrimental to mites (70).

Phosphorus: In forest soils, phosphorus alone or combined with other elements stimulated acarine population (87, 144). Ronde (190) found that when lime plus phosphorus was used, there was a 2.5-fold increase in fungi, which seemed to benefit more than the bacteria from the phosphorus. Consequently, the Oribatei, some of which are known to feed on fungi, also increased.

Potassium: Five years after fertilizing a red pine plantation with 448 kg K/ha of potassium chloride, the four major Orders of mites (Astigmata, Mesostigmata, Cryptostigmata and Prostigmata) increased by 59, 25, 12 and 3.5%, respectively, over controls (33). However, the total

number of families decreased in the fertilized plots, indicating a differential response by families and possibly species.

Calcium: Liming increases mite numbers under agricultural conditions (55, 70), but forest soils behave differently because food and living space of the mites are reduced with the accelerated decomposition of the litter. Initial increases in forest soils (87, 144) are also associated with changes in species distribution and composition; the Cryptostigmata are generally adversely affected. Ronde (190) found that 2 years after liming and planting lupines, Mesostigmata and Prostigmata increased. She listed the dominant Cryptostigmata on unlimed plots as Belba sp., Cepheus sp., Hermanniella granulata (Nicolet, 1855), Hermannia gibba (C.L. Koch, 1839), Galumna sp., Hypochthonius sp., Liacarus xylariae (Schranck, 1803) and Nothrus silvestris Nicolet, 1855 , whereas on limed plots, Carabodes sp. and Tectocepheus sp. predominated. Franz (67) also noted a reduction, from 39 to 33, of oribatid species 4 years after liming. Adoristes obovatus (C.L. Koch, 1839) increased slightly during this period, but Carobodes labyrinthicus (Michael, 1879) and T. velatus showed a progressive yearly reduction.

Earthworms frequently replace microarthropods as the primary faunal decomposers when forest soils are limed. Litter feeding Oribatei such as Rhysotritia duplicata (Grandjean, 1953) and Rhysotritia minima (Berlese, 1904) and fungal feeders like T. velatus disappeared almost completely, but Steganacarus spinosus (Sellnick, 1920), which feeds on materials ignored by earthworms, may be unaffected (142).

Various authors (14, 67, 168, 190) have presented sufficient data

to permit an analysis of long-term effects from lime applied at 2 to 10 t CaO/ha. During the first decade there was no obvious trend in population increases or decreases, nor were population changes statistically significant from controls. However, 28 years after applying 10 t CaO/ha to forest soils, the Mesostigmata and Cryptostigmata were reduced by 50 and 42%, respectively, from controls (70). A tendency was also noticed for a larger proportion of individuals to occur lower down the soil profile. The ratio of individuals between the top 4 cm and the next 4 cm for the Mesostigmata were 16: 1 and 6: 1, and for the Cryptostigmata were 175: 1 and 30: 1 in unlimed and limed plots, respectively.

Trace elements: Fertilizers containing copper and molybdenum applied to pastures inhibited oribatid development, primarily nymphs in the families Camisiidae, Galumnidae, Oppiidae and Scheloribatidae (131). "Blue copperas" applied at 15 to 25 kg/ha produced a 4- and 6.6-fold decrease in oribatid population during the first and second year after application, respectively. Nymphs in ammonium-molybdate treated plots also were two and a half times fewer than in controls.

OTHER ANIMALS

Manures

Farmyard manure increased amoebae populations 4 to 7 times over unmanured plots (4, 217). Jobling (111) theorized that mulching may provide nests for moles, but there is no evidence that manuring increases mole populations.

Fertilizers

Most of the other soil animals seem to benefit from, or at least are unaffected by fertilization. Increases have been observed for protozoans (217), molluscs (132), isopods (22, 144), opiliones (14) and miscellaneous arthropods (18, 242). Moles are probably adversely affected by high rates of ammonium nitrate limestone, as Ennik (56) found that there were four times more mole hills in grazed plots receiving 70 as opposed to 140 kg N/ha; mole distribution was not correlated with earthworms, which form a major part of the mole's diet (46, 51, 202) but is not its exclusive food (236).

NATURE OF EFFECTS INDUCED BY MANURES AND FERTILIZERS

Although species behave differently, manures and fertilizers generally increase faunal populations and the magnitude of response varies with species, major taxonomic groups and type of amendment. Nearly all groups (Table 1), especially those containing large numbers of saprophages (nematodes, earthworms and diplopods), increased substantially in numbers following manuring.

Except for spiders, the majority of soil animals also respond positively to most fertilizers (Table 2). However, under agricultural conditions, continual use of monocalcium phosphate (151), superphosphate with sodium nitrate, and ammonium sulphate (100) depress some soil fauna. Like agricultural soils, fertilizing forest soils with acid-forming sulphates does not apparently stimulate maximum increases of soil animals

increased numbers of species and individuals (69, 74, 122, 221, 225, 226), but the highest rates of increases have come from complete and mixed fertilizers (99-101, 157, 192, 225), especially when calcium accompanied these fertilizers (222). Other soil amendments used for counteracting alkalinity or salinity, e.g. sulphur, ammonium and iron sulphates and gypsum, usually produce conditions favouring greater numbers and diversity of fauna (116).

Table 3 summarizes various authors' data and shows the response of individual groups as well as many groups combined to the two types of amendments. Manures seem to be more effective in increasing the fauna, but they did not always produce the highest numbers. The response from a combination of manures and fertilizer is usually additive, only slightly surpassing that produced by either amendment applied alone; however, a synergistic effect, from combining the two amendments, was obtained for diplopods (90) and insects (151). Where manures or fertilizers alone produced higher populations than both amendments combined, the differences were insignificant and short-lived (64), affected by cultural practice, animal species (95, 98, 118, 124), type of fertilizer (151) and climatic conditions (100).

Despite the basic differences between manures and fertilizers discussed heretofore, several general observations allow their actions to be classified as: (a) immediate and direct effects, and (b) delayed indirect effects.

Direct Effects

Substances present in manures and fertilizers, or their breakdown products, are toxic to soil fauna. Also, manures and fertilizers may change soil pH, water status and osmotic potential, all of which directly affect soil animals.

Manures: Liquid manure increases soil water and directly affects the soil fauna by reducing mites, particularly Mesostigmata, and by changing the qualitative composition of nematodes, mites and springtails to species more characteristic of wet environments (85, 86). Other manures may initially reduce the fauna (94, 179), but they usually have a beneficial effect by (a) introducing organisms not previously present in the soil (150, 223), (b) adding to the food supply of coprophagous or saprophagous species and thus their dependents (53, 116), and (c) increasing living space and improving the water-holding capacity of the soil (157, 207).

Fertilizers: Kuhnelt (125) suggests that species composition and density decrease with increasing salt content, which indicates a possible adverse effect from high rates of inorganic fertilizers. Such a detrimental effect is apparent from the immediate reduction or "shock effect" by some fauna following fertilization (18, 100, 102, 103, 132). Huhta et al. (103) believed that the fertilizer itself or adjunct impurities (e.g. S and Cl) act as a poison. Gaseous ammonia, applied at 200 kg N/ha, virtually sterilizes the soil (57, 65) and ammonia is toxic to nematodes, earthworms, mites, myriapods, insects and isopods (125, 153, 154, 188, 198). Besides ammonia, other transformation products of nitrogenous compounds

may be nematicidal (112, 172, 231, 232). Both complete fertilizers and urea depress enchytraeid populations, and for Cognettia sphagnitorum this effect is long-lasting (2), indicating that more than a shock effect is involved. The detrimental effects of sulphates and phosphates have already been discussed under earthworms and although the lethal agents have not been identified with certainty, pH changes and possibly hydrogen sulphide production, among other factors, appear to be important.

Initial reduction of mites by calcium cyanamide (100) and urea (18) is probably related to ammonia, as it is a major decomposition product of both these fertilizers. Excessive ammonia production from urea is to be expected at high pH ranges but is also possible at low pH ranges (44), especially at high temperatures and during dry, windy conditions. Many soil animals excrete urea as a waste product of nitrogen metabolism. Urea is also one of the solutes, with water and glycerol, that moves freely through a membrane (194). Therefore, soil animals could conceivably ingest or absorb this fertilizer directly in sufficient quantities that could not be safely excreted, causing death by urea poisoning or by affecting enzymes.

Trace elements of copper and molybdenum are very toxic to oribatid nymphs (131). Soils contaminated with high copper residue appear to be harmful to earthworms (54, 163, 181, 184), and even low copper concentrations are toxic to some nematodes (40, 175).

In recently fertilized soils, the osmotic effect might be high enough to damage soil fauna, but this has been little studied. According to Viglierchio et al. (228), osmosis may injure nematodes in three ways:

(a) irreversible dehydration, (b) toxicity of chemicals in hypertonic solutions, and (c) excessive uptake of water after regulation in hypertonic solutions, resulting in body rupture. Ditylenchus dipsaci (Kühn, 1857) Filipjev, 1936 larvae were killed by a 1 M urea solution, or 22.4 atm osmotic pressure (23), and hypertonic solutions of similar concentrations reduced the mobility of Rhabditis spp. (228), and delayed hatching in Meloidogyne javanica (Treub, 1885) Chitwood, 1949 , Meloidogyne arenaria (Neal, 1889) Chitwood, 1949 and Heterodera rostochiensis Wollenweber, 1923 (50). However, nematodes vary in their ability to withstand hypertonic solutions and some species may tolerate 20 atm osmotic pressure for 24 hours without showing much loss in subsequent mobility (234). Also, the osmotic potential itself, compared to total water potential, may not have much effect on nematodes (23). Rates of 800 kg N/ha is not expected to produce more than 5 atm in the top layer of the soil (29, Marshall, unpub.); therefore, the osmotic potential is probably not important in reducing faunal numbers following low rates of fertilizer application. At higher rates of some fertilizers, which dramatically reduce faunal numbers, it would be difficult to separate detrimental osmotic effects from toxicity by noxious gases as the prime cause of mortality.

Indirect Effects

The indirect effects of manures and fertilizers on soil fauna are complex, subtle and sustained. Changes are brought about mainly by altering the C:N ratio and pH of the soil which, in turn, greatly influence the micro- and macroflora that are the primary source of food for the fauna. In addition, excessive quantities of sodium and chlorine in fertilizers,

which destroy crumb structure (157), may affect the fauna. The nature of these changes vary with different soil conditions and the extent to which they affect the soil fauna is manifested in seasonal fluctuations, vertical distribution and duration of response.

Soil reaction: Apart from calcium, usually used to correct excess soil acidity, some fertilizers such as nitro-chalk, nitrate of soda, calcium nitrate and calcium cyanamide may be neutral to basic in effect, whereas others like ammonium sulphate are usually acid forming compounds. Adjuncts in the main formulation may produce decomposition products that change soil reaction, as with sulphuric acid formed from superphosphates. Nitrogenous fertilizers, used alone, may initially increase pH, but they eventually create acid conditions in neutral soils if the nitrogen is oxidized to nitric acid. The resulting composition and activity of the microflora is governed by the type of changes induced by the fertilizer (173).

More species of algae, bacteria and actinomycetes occur in neutral to slightly alkaline soils, whereas fungi predominate in acid situations. Alexander (4), however, emphasized that this does not mean that fungi find their optimum at low pH values but, rather, they flourish there due to a lack of microbial competition for available food. Thus, physiologically neutral and basic fertilizers, or those that correct a nutritional deficiency, tend to increase total microfloral populations (37, 65, 68, 134, 135). Soil pH also affects availability of essential nutrients to higher plants and thus their productivity and resultant quantity of food for the fauna.

Microflora: Manures and fertilizers supply a ready source of nutrients that permit the rapid multiplication of the microflora (4, 186, 187, 199, 208) and intricate and complex relationships exist between the soil microflora and fauna (30, 38, 48, 55, 138, 139). Odum (166) recognized eight important types of interactions between two species (neutralism, competition, mutualism, protocooperation, commensalism, amensalism, parasitism and predation), all of which occur between the microflora and the soil fauna (147). For oribatid mites, complicated relationships, which may be at several levels, occur with soil microflora (136). The microbes act as a dietary component of the mite's food or as a physical conditioner, rendering the litter more palatable. Apart from essentially microphagous species, other fungi-feeding forms do not appear to digest an important fungal carbohydrate (trehalose), but their feeding provides a readily degradable product replete with viable microbes. Other mites disseminate fungal spores and enhance fungal growth by cleaning away antibiotic-producing fungi. This "sanitation" process permits attack by the next group of microbes in the succession. Such faunal-flora-interrelationships make it very difficult to evaluate the effects of increases in the microflora on the soil fauna. However, faunal increases may be expected, as many species of every major soil-animal group, including thecamoebae, slugs, snails, nematodes, mites, myriapods, springtails and other soil insects, are microphytophages (31, 125, 182, 237). Carnivorous, macrophytophagous, saprophagous and miscellaneous feeders would also benefit from increases in prey and plant production resulting from fertilization.

Macroflora: Fertilizers indirectly influence soil fauna by

affecting the surface flora, as some animals feed on plant roots and decaying plant material, whereas others may be specifically associated with certain plant genera or species. Many authors have shown a relationship between plant yield and density of free living soil fauna (95, 98, 100, 132, 203, 215) and some nematodes, among the macrophytophagous root feeders, also benefit from increased plant growth (88, 120). Earthworms appear to take advantage not only of herbage changes and increased litter (20, 36, 82, 110), but also greater root production (107, 132, 238). Better shading may increase earthworms and other members of the fauna (101, 107), but the reverse is true for some ants (132).

Seasonal fluctuations: The effects of manures and fertilizers in changing the pattern of seasonal fluctuations are not well documented. However, in cases where the "shock effect" was not very detrimental, populations of nematodes and collembolans in agricultural soil tended to peak before controls, during the first year after liquid-manure application (86). Also, population peaks of Collembola, which occurred under grass or fallow only in autumn, shifted to summer following manuring (98) and grass mulching (96). Since faunal increases by fertilizers is brought about mainly through indirect effects, a similar shift as for manures is not expected to be common, although Gusenleitner (86) observed an earlier nematode population peak in superphosphate-treated than in untreated agricultural soil.

Vertical distribution: Manures and fertilizers alter the vertical distribution of the fauna, but different mechanisms are probably involved for each type of amendment. In agricultural fields, an undisturbed

soil exhibits a gradual decrease in numbers with increasing depth; the ploughing-in of organic material modifies the vertical distribution, as more animals can survive at deeper depths (160). Manuring likewise changes the normal pattern, permitting a larger proportion of animals to survive in deeper layers of the soil than in an undisturbed profile (95, 98, 150, 243). The depth at which the material is incorporated in the soils seems important, and Tischler (223) states that the biological effect is more favourable at 5 to 10 cm than at 15 cm. In mor-type forest soils, fertilizers that contain calcium, or those that stimulate macrofauna, promote the rate of decomposition and tend to become a self-accelerating process as deficient elements are cycled in the ecosystem. This causes an alteration of the faunal composition from an arthropod-dominated system to one where earthworms, in particular, play a greater role (70, 142). Accompanying these changes is a shift in the microarthropod fauna to lower horizons as the litter is gradually incorporated in the soil. Urea, an excellent dispersant of organic matter (241), also affects the distribution of enchytraeids (2), mites and collembolans (18) by reducing the numbers in the litter layer; this is partly due to a downward migration of some litter populations and death of other litter fauna.

Duration of Effect

The relationships of the various soil organisms are in a state of flux, and the observed composition of a population in a habitat is governed by the biological equilibrium created by the associations and interactions of all individuals in the population (4). It is within this context that the response of the soil fauna to manures and fertilizers

must be interpreted. These amendments disturb the equilibrium, creating oscillations of varying frequencies and amplitudes; in some cases, the equilibrium is restored quickly (e.g. 57, 86, 94, 132, 179, 248); in others, the population permanently shifts to take advantage of the new circumstances (e.g. 69, 142), with faunal increases occurring gradually over many years (103).

The initial large population resulting from manuring gradually declines if fresh material is not added, but differences between manured and unmanured plots may still be evident 10 years after application (157). However, each group responds differently. For the mites, the beneficial effect may last less than 3 years (95); for the nematodes, enchytraeids and collembolans, as many as 10 years (64).

Continuous fertilization over 50 years did not adversely affect the fauna (53) and fertilizers may benefit the fauna in the short term (Tables 1 and 2). Even initial reductions were counterbalanced by subsequent larger populations (18, 86, 132). Positive responses apparently common from 3 to 15 years after fertilization (1, 103, 225) may persist for many more years, depending on the animal group and type of fertilizer. Franz (64) noticed a positive effect for enchytraeids, collembolans and mites 10 years after the application of NPK. The favourable effects on earthworms, especially by fertilizers containing calcium, may range from 11 to 23 years (20, 49).

CONCLUSIONS

The general awareness of the importance of soil fauna as plant

pests and to nutrient cycling has been accompanied, in the past two decades, by numerous articles on the effect of manures and fertilizers on soil animals. These studies reveal: (a) although certain formulations may adversely affect a specific group of animals, manures and fertilizers generally increase numbers and species of the soil fauna; (b) manures do this directly by adding fauna and by providing food for coprophagous and saprophagous species; (c) manures, like fertilizers, have an indirect effect by increasing prey for carnivores, changing the soil structure, and increasing the growth of micro- and macroflora on which the fauna feed, and (d) both amendments add substances or produce conditions that may temporarily reduce faunal populations. The toxic agent has not been identified in all cases, but additions of "poisons", changes in pH and production of noxious gases appear important. (e) Such reductions are usually counterbalanced by large increases at a later date; (f) if species changes are disregarded, the favourable effect on numbers may last from 10 to 20 years; (g) there is usually an alteration in the vertical distribution and a successional change in appearance and dominance of various faunal groups and species following manuring and fertilization, and (h) although liming may irreversibly change forest soil fauna, only the superphosphates and the sulphates, when they produce acid conditions, appear to have a potential for permanently reducing faunal populations, particularly earthworms.

The significance of these changes depends on a stated objective, but from the viewpoint of soil faunal well-being and plant productivity, manures have been beneficial without generally increasing plant pests.

Assuming adverse side-effects from heavy metals, parasites and pathogens are controlled in urban wastes, the indication that organic amendments depress plant-parasitic nematodes while they increase saprophagous members of the soil fauna could be advantageous to those who wish to return sewage-derived and other similar organic wastes to the soil.

The effects of inorganic fertilizers on noxious insects and diseases are extremely variable and each problem may have to be considered individually (32, 145, 146, 241), but so far the results from intensive use of fertilizers have been mainly positive (60, 91). The recognition that potassium affects nematode plant-host relationship and that lime and nitrogenous fertilizers depress parasitic nematodes could be of immense practical importance. Pest control alone will rarely justify the use of manures and fertilizers, but the extra bonus from pest reduction could prove valuable in many situations, and deserves further attention.

The tendency for a shift in some forest soils from an essentially microfaunal system to one in which the macrofauna, especially earthworms, play a more dominant role is generally desirable as the ecological efficiency is increased (140).

Many serious difficulties still remain. Soil fauna show a high degree of aggregation in spatial distribution and pronounced variation in seasonal abundance, which requires about a 200% change from controls to demonstrate real treatment effects with practical numbers of samples. To show differences between fertilized and unfertilized plots with statistical reliability, large numbers of samples are often required. Behan's (18) estimate of 850 samples per sampling date to show statistically significant

results must be the highest limit, but it clearly underlines the problem. So far, many results have been based on high taxonomic groups, but the abundance of a particular species may change while the abundance of the group may be unaltered. As the reduction of some species may be ecologically compensated for by increases in others, analyses should be done at the species' level and these should be supported by detailed information on the biology and ecology of affected species. There is also the need to measure changes in other parameters such as ATP production, faunal biomass, soil respiration, and energy and nutrient flow.

In forest soils, initial fluctuations of each group might be widely scattered points on a curve that is oscillating toward a more stable equilibrium; therefore, there is a need for long-term investigations. Important areas of research should include the mode of action of fertilizers on faunal mortality, the types of fertilizers that would allow advantageous manipulation of soil animals, and studies that would lead to a better understanding of the complex relationships between flora and fauna.

Manure and fertilizer rates, currently used, are usually beneficial to the soil fauna; however, Franz and Loub (70) have already advised that physiologically acid nitrogenous fertilizers should be discouraged for acid forest soils unless calcium is also added. In addition, excessive applications of fertilizers for accelerating natural thinning of dense forest stands, for possible control of root diseases and for cone production in seed orchards are situations that require study. Edwards (52) stated that "although we can speculate on the long-term

ecological effects of pollutants, we cannot precisely determine the ultimate consequence of much reduced numbers of soil animals until we fill gaps in our knowledge of the various roles played by the different species of invertebrates in the soil." The same could be said of changes induced by manures and fertilizers, as we do not know what levels, combinations or frequency of application will permanently alter adversely the soil ecosystem. Therefore, considerable intensification of research is necessary in basic soil biology and on the complex interactions between manures and fertilizers and soil fauna, if soil zoology is to make further major contributions to the proper management of agricultural and forest ecosystems.

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TABLE 1. Response, expressed as a per cent of control, of various groups of soil animals to manures and manures plus inorganic fertilizers.

Treatment	Habitat	Nema-todes	Earth-worms	Enchy-traeids	Diplo-pods	Symph-ylids	In-sects	Collem-bolans	Mites	Spi-ders	Reference	
Manure	Arable	450+	220	-	329	-	695	344	246	-	(150)	
Manure	Arable	3194+	4173	-	948	387	253	417	700	65	(151)	
Manure	Arable	750	433	-	221±	-	552	144	342	243	(197)	
Manure	Arable	325	-	255	-	358	200++	206++	129	75	(100)	1954 data
Manure	Arable	-	-	150	186	-	115	236	191	-	(206)	
Manure	Arable	-	-	-	-	-	-	232	203	-	(53)	
Manure	Grassland	91	-	770	-	-	-	190	129	-	(64)a	
Manure	Grassland	202	-	400	-	-	-	640	66	-	(64)b	
Manure + NH_4 salts	Arable	1798	2696	-	378	575	898	537	300	135	(151)	
Manure + $Ca(H_2PO4)_2$ + NH_4 salts	Arable	1763	2426	-	1075	387	221	413	548	135	(151)	
Manure + NPK	Grassland	164	-	749	-	-	-	168	86	-	(64)a	
Manure + NPK	Grassland	162	-	1040	-	-	-	315	116	-	(64)b	

+ = Oligochaeta limicolae; ++ = Apterygota
++ = Pterygota; ± = Myriapods

a, b = One and 10 years after application, respectively.

TABLE 2. Response, expressed as a per cent of control, of various groups of soil fauna to inorganic fertilizers.

Treatment	Habitat	Nema-todes	Earth-worms	Enchy-traeids	Iso-pods	Diplo-pods	Symphy-lids	In-sects	Collem-bolans	Mites	Spiders	Reference
NPKCa	Arable	174	-	106	-	-	214	113	178	178	80	(100)a, 1954 data
NPK	Arable	191	-	103	-	-	86	125	148	102	25	(100)a
PK	Arable	278	-	70	-	-	57	156	100	119	25	(100)a
NK	Arable	270	-	70	-	-	43	137	146	135	25	(100)a
NP	Arable	138	-	12	-	-	100	50	104	76	55	(100)a
$NaNO_3$	Arable	200	-	155	-	-	28	199	118	91	25	(100)a
$CaCN_2$	Arable	183	-	136	-	-	174	100	123	93	10	(100)a
NH_4 salts	Arable	152+	65	-	-	15	-	340	169	475	35	(151)
$Ca(H_2PO_4)_2$	Arable	93+	-	-	-	15	-	63	326	26	35	(151)
$(NH_4)_2SO_4$	Arable	9	-	0	-	-	71	106	102	38	14	(100)a, 1954 data
NPK	Grassland	93	-	100	-	-	-	-	202	101	-	(64)b
NPK	Grassland	79	-	200	-	-	-	-	273	139	-	(64)c
NPKCa	Spruce forest	92	11	82	-	-	-	81	158	115	93	(102)d
NPKCa	Spruce forest	-	-	180	-	-	-	-	88	118	-	(103)e
NPKCa	Spruce forest	175	333	165	167	120	-	225	156	222	-	(144)f
NPKCa	Pine forest	363	3600	74	200	1300	-	600	177	248	-	(144)f
NPK	Beech forest	436	1200	282	700	535	-	1000	166	262	-	(144)f
NPK	Oak forest	300	575	322	250	240	-	225	175	440	-	(144)f
$CaCO_3$	Spruce forest	79	2800	-	-	-	-	-	126	92	-	(70)

a = Hryniuk's (100) Pterygota listed here as Insects and Apterygota as Collembolans.
+ = Oligochaeta limicolae.
b and c = One and 10 years, respectively, after application.
d and e = Three and 5 years, respectively, after application.
f = Mayer-Krapoll's (144) myriapods listed here under diplopods.

TABLE 3. Response of different groups of soil animals to organic and inorganic fertilizers in agricultural soils. The numbers represent authors in the references who observed the sequence.

	O>I	I>O	IO>O>I	IO>I>O	O>IO>I	O>I>IO	I>O>IO
Nematodes	92,100,157,177,246	100,157	195	64	64		
Earthworms	92		118,243	118	151		
Enchytraeids	92,100	100	64,118	118	64		
Myriopods	92,100	100	90,151	118	151		
Insects	100		151	118			
Collembolans	53,92,100,157	100,157	118,151,195	98,118	64		64
Mites	53,92,157	100,157	64,95,151		151,195	64	
Many Groups	100,178,195	100					

I = Inorganic fertilizer.

O = Organic fertilizer.

IO = Inorganic + Organic fertilizer.